

DOMINANCE-SUBORDINATION IN CAGED GROUPS OF HOUSE SPARROWS

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ORNITHOLOGISTS long have been intrigued with the behavioral mechanisms which tend to promote gregariousness and precision of flock activities (Emlen, 1952; Moynihan, 1960; Crook, 1961). Dominance-subordination relationships in gregarious species have been studied by a number of workers (Masure and Allee, 1934; Shoemaker, 1939; Ritchey, 1951; Sabine, 1959; Thompson, 1960; and Ellis, 1966) to name but a few.

The behavioral mechanisms operating in the maintenance of gregariousness in the House Sparrow (*Passer domesticus*) have received little attention. The possibility that dominant individuals act to synchronize group activities in large foraging flocks of House Sparrows was suggested by Summers-Smith (1963). Some aggressive characters in a flock of color-marked House Sparrows were studied by Simmons (1954) but he made no statements on the dominance structure of the flock.

Since this species occurs commonly in large flocks, observations of dominance-subordination relations and behavioral cycles are made difficult by the diversity of flock activities. However, if a dominance structure exists, it should be evident in small flocks subjected to intensive study. Accordingly, groups of House Sparrows were assembled in order to study the various aspects of dominance-subordination under captive conditions.

METHODS

Eight groups of House Sparrows totaling 52 individuals were taken at various locations in and around Logan, Utah, between January and September, 1965. The groups contained 8, 8, 4, 6, 6, 8, 6, and 6 individuals, respectively. No more than two individuals of any group were taken from any one locality, thus minimizing the influence of previous interactions. Excepting one group (Table 2), no individual was used in more than one experiment. Members of each group were individually color marked and released into the aviary simultaneously. Two separate, visually isolated aviaries measuring $9 \times 7 \times 10$ feet were utilized in the study.

Constant 12-hour photoperiods were maintained through the use of an automatic light timer installed after April, 1965. Observations were made through tinted glass.

Each aviary was supplied with a perch graduated at one-inch intervals, a simulated tree perch, a water can, and a large floor feeder (a wooden tray, 18×36 inches). Millet was provided ad libitum and meal worms (*Tenebrio*) were occasionally used.

The observation periods were rotated daily on a systematic basis ("morning," "afternoon," and "evening") in order to compensate for cyclic behavior fluctuations.

Both first-year and juvenile birds were included in this study (Table 1, groups 3, 4, 6.

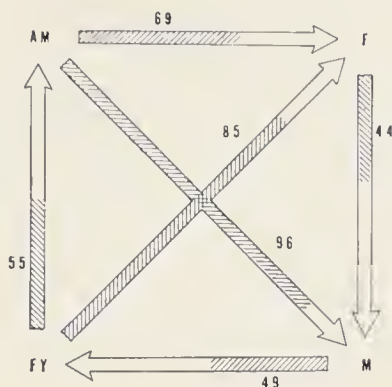


FIG. 1. Relative dominance between four classes of House Sparrows. Cross-hatching indicates the percentage of encounters won. For example, first-year birds were dominant to adult females in 85 per cent of the contests. Based on the dominance-subordination data from groups 1-7 (Table 1). Key: AM—Alpha Male; F—Adult Female; M—Adult Male; FY—First-Year (A composite of first-year and juvenile birds).

and 7). First-year birds are those which completed the post-juvinal molt and still show incomplete skull ossification. However, I will refer to both age classes as first-year birds; exact designation will be given in the tables.

Social ranking was determined through dominance and subordination responses (i.e., supplanting by the dominant bird and subsequent withdrawal by the submissive) at the feeder, water can, and perches. Threat displays resulting in spacing were not recorded as a "win" or "loss." Dominance and subordination were tested using the chi-square test with a 2×2 contingency table (Ostle, 1963). The correction for continuity was used on 2×2 tables. The percentages of wins were compared for each bird in each group.

Additional information was obtained by observing free-living flocks of House Sparrows at two locations outside Logan, Utah, from March, 1965, through September, 1965. One flock numbering around 100 individuals contained 37 marked birds.

RESULTS

Dominance and subordination.—The general pattern of interactions is shown in Figure 1. Each group under observation included a dominant adult male (Tables 1-2). Although no straight-line social rank system was present, I will refer to the individual having the highest number of wins as the alpha male. Due to the presence of this more combative bird (see beyond), all groups were highly significant (99 per cent level) with respect to the percentages of wins. Analysis showed significant differences (95 per cent level) between this more combative bird and other flock members. Three exceptions occurred (Table 1, groups 3 and 4; Table 2, 8b, 8c, and 8e). Groups 3 and 4 (Table 1) included first-year birds. First-year males secured high percentages of wins through successful encounters with the alpha male (Figure 1, Table 4). Simmons (1954) stated that he found "juvenile" House Sparrows to be regularly very pugnacious over food, holding their own not only with adult House Sparrows but sometimes against Starlings (*Sturnus vulgaris*). Similarly, Thompson

TABLE 1
THE PERCENTAGES OF WINS OF 7 GROUPS OF CAPTIVE HOUSE SPARROWS

Groups	Alpha Male	Male	Male	Male	Female	Female	Female	Female
1 2-29 January 1965								
Per cent of Wins	85 (843)	41* (285) ¹	14* (319)	9* (282)	64* (160)	67* (135)	33* (151)	16* (153)
2 6-19 February 1965								
Per cent of Wins	92 (472)	14* (367)	34* (121)	24* (144)	50* (70)	52* (48)	33* (57)	49* (35)
3 1-20 April 1965								
Per cent of Wins	93 (378)	38* (164)	11* (372)	fy ² 67* (30)	sfy ² 56* (36)	17* (12)	—	—
4 7-22 May 1965								
Per cent of Wins	87 (198)	15* (124)	32* (66)	fy ² 64 (58)	20* (35)	8* (39)	—	—
5 9 June-6 July 1965								
Per cent of Wins	83 (551)	11* (311)	41* (169)	36* (100)	34* (86)	40* (62)	40* (60)	29* (21)
6 30 July-18 August 1965								
Per cent of Wins	84 (306)	44* (122)	12* (177)	juv ² 56* (104)	20* (49)	4* (46)	—	—
7 11 September-4 October 1965								
Per cent of Wins	82 (319)	30* (233)	40* (154)	juv ² 94 (137)	15* (59)	69* (118)	—	—

¹ Number in parentheses is the size of sample.

² fy = first year; sfy = suspected first year; juv = juvenile.

* Significant differences from Alpha Male (0.95 level).

(1960) stated that in the wild, "juvenile" House Finches (*Carpodacus mexicanus*) often won encounters over adults of the same species. Inspection of groups 3 and 4, and 7 shows high percentages of wins for the first-year birds relative to the alpha male. However, marked differences occur when one compares the total number of encounters between the two birds (alpha and first-year). Therefore, regardless of this result, the alpha male was still the more combative bird.

TABLE 2
CUMULATIVE PERCENTAGE OF WINS OF 2 GROUPS OF CAPTIVE HOUSE SPARROWS

Groups	Male (A)	Male (B)	Male (C)	Male (D)
8a. 23-28 April 1965				
Percentage of wins	76*	24**	—	—
8b. First two hour observation period, 29 April 1965, males C and D are from group three (Table 1) having previous win-loss ratios of 0.9259 and 0.1129 respectively.				
Percentage of wins	92*	100	4**	0**
8c. Second two hour observation period on 30 April 1965				
Percentage of wins	69	100	50	0
8d. Third two hour observation period on 1 May 1965				
Percentage of wins	23**	0**	96*	0**
8e. Fourth hour observation period on 2 May 1965				
Percentage of wins	25**	100	76*	0**

* Denotes alpha male.

** Significant difference from alpha male (0.95 level).

Characteristically, the alpha male initiated the aggression against the first-year birds. Once attacked, the first-year males—and in one case a suspected first-year female (Table 1, group 3; Table 3)—demonstrated marked abilities of self-defense, often assuming the hen threat posture illustrated by Summers-Smith (1963, Fig. 2). The first-year birds never pressed the attack, but merely refused to leave their positions even if actual fighting contact occurred. Similar behavior occurs in Blue Tits (*Parus caeruleus*) in which feeding birds show a tendency to stay and threaten intruders in lieu of overt attack (Stokes, 1962). Uinta ground squirrels (*Citellus armatus*) involved in maintenance activities also demonstrated this “stay threat” behavior (Balph and Stokes, 1963). “Stay threat” behavior was more pronounced in juvenile ground squirrels than adults (Balph, personal communication). Also, “stay threat” response was more intensely displayed by first-year House Sparrows than by adults of the same species.

The alpha male defended the simulated tree perch, the marked perch, and the elevated water can. At night the remaining males were forced to use the floor or to cling to the tiled ledges for perch (roost) sites. The females and first-year birds generally roosted on the floor but sometimes they remained on the elevated perches with the alpha male.

Examination of Tables 3 and 4 shows the alpha male directing a great number of attacks toward one specific adult male. This male maintained no spe-

TABLE 3
INDIVIDUAL ENCOUNTER DATA FROM THE APRIL GROUP (TABLE 1, GROUP 3)

Bird	Alpha Male A	Male B	Male C	First Year Male D	First Year Female E	Female F
		Loss				
A		66	268	4	10	2
B	6		56	0	0	0
C	0	34		4	2	2
Win						
D	6	2	2		4	6
E	14	0	4	2		0
F	2	0	0	0	0	

cific site and thus was subject to constant attacks from the alpha male. The remaining adult males secured isolated sites at which they remained (unless feeding or drinking), and which they actively defended. These sites were not associated with any perching device in the aviary but were situated in the far left corner (from entrance) of the aviary 75 inches from the floor level on a ledge atop the tiled portion of the wall. The adjacent right corner was only 6 inches from the elevated perch and hence was defended by the alpha male. At these specific sites, the alpha male was subordinate.

In groups 1, 2, and 5 (Table 1) the site problem was more acute due to the presence of four adult males. In each of these groups, an adult male remained on the wall thermostat which was situated only two feet from the elevated perch. This position offered some protection from the alpha male and usu-

TABLE 4
INDIVIDUAL ENCOUNTER DATA FROM THE AUGUST GROUP (TABLE 1, GROUP 6)

Bird	Alpha Male A	Male B	Male C	First Year Male D	First Year Female E	Female F
		Loss				
A		56	140	24	22	14
B	22		6	10	10	6
C	2	8		4	0	8
Win						
D	26	4	9		8	9
E	0	0	0	0		2
F	0	0	2	4	4	

ally ensured its occupant of an elevated roost overnight. Again, the male receiving the majority of defeats had no specific site to defend.

The flocks tended to remain in only one half of the aviary even though perching devices were placed at the opposite end. The area in which the flocks remained contained the food and water trays. Birds flying to the far end of the aviary were quick to return to the flock. Similar behavior was reported for *Quelea quelea* by Crook (1961). The subordinate males did not utilize the far corners for roost sites. Seemingly, the attraction of the group had priority over the effects of subordination.

Status of females and first-year birds.—As shown in Figure 1, adult females were subordinate to the other classes of sparrows. This was due, in part, to their tendency of readily submitting to aggression on the perches. The females initiated few direct agonistic encounters. Their fights per hour averaged 1.3, whereas adult males averaged 8.2 fights per hour. This last figure is somewhat distorted, however, due to the activity of the alpha male. Normally, males would not attack females unless they crowded too close on the perches or in the feeder. Attacks upon females by males were of low intensity and rarely included physical contact. Many times the females would merely space out, this action being sufficient to halt the male aggression. However, adult females were dominant over adult males in 44 per cent of the encounters (Fig. 1). In contrast, male attacks upon males invariably necessitated one or the other leaving the immediate site. The first-year birds tended to remain with the adult females and were treated as females by adults of both sexes.

The alpha male characteristically made direct, sudden attacks upon the adult males with little preliminary display given. However, his attacks upon females and first-year birds were of a threat nature, followed by direct attack only if the recipient failed to respond by moving away or by showing submissive behavior.

Because they had not yet completed the post-juvenal molt, the juveniles (Table 1, groups 6 and 7) closely resembled the adult females in appearance and (as indicated above) were treated as adult females. This similarity of juvenal plumage to that of advanced first-year or adult female House Sparrows has been described by Selander and Johnston (1967). The two first-year males (Table 1, groups 3 and 4) showed a variable amount of white tipping to the black chin feathers, and the pileum had a brownish hue, rather than gray of the adult male.

As stated previously, "stay threat" behavior was characteristic of both juvenile and first-year birds. The results of "stay threat" are reflected in the high win success as indicated in Figure 1. This pugnacity seems functional, for these young birds can defend against intruding adult males while feeding and

perching. These early aggressive encounters undoubtedly contribute to the fitness of young birds by providing valuable fighting experience prior to their first breeding season.

Manipulation of birds.—One experiment was conducted with two males designated A and B, respectively. A was dominant over B (Table 2, 8a) having 59 wins to 19 wins for B. On 20 April 1965, I released two birds from the April group, the alpha male designated C and a subordinate male designated D (Table 1, group 3) with A and B. During the first two hours of observation, A defeated C 94 times, illustrating how familiarity with an area can influence the outcome of aggressive encounters. Similar results were reported for caged groups of House Finches by Thompson (1960). D, who had lost all previous encounters with C, was successful in defeating C 19 times on the perches. Two factors seemed to be involved. When the alpha male would rapidly displace one individual about the aviary, others might also join in and displace the recipient. The recipient, under these conditions, would readily give way to any aggression directed towards him. There seemed to be an “aggressive momentum” operating first in the attack by the alpha bird, and subsequently spreading to the other flock members. Correlated with this was a tendency towards heightened submission by the bird subjected to these rapid attacks. Another factor was that C, who previously had maintained a large defended area, now was without one in strange territory.

On the third day, C was ahead of A with percentages of 96 and 23, respectively, indicating a reversal of dominance (Table 2, 8d). This relationship held until the sixth day, when A was discovered dead.

Flock activities.—Within certain limitations, synchronization and integration within the flocks followed an intrasexual pattern. However, the first-year birds tended to remain with the adult females and were treated as females by adults of both sexes. Figure 2 represents a sample recording of group activity cycles from a well-stabilized flock at four times over the course of one photoperiod. The figures show that the individuals tended to be engaged in the same activities at the same time, much as shown for *Quelea quelea* by Crook (1961).

Despite uniformity of photoperiod (constant 12 hr) and temperature, a definite daily activity pattern was present. Figure 2 illustrates this phenomenon. The greatest amount of active behavior (e.g., feeding) occurred in “morning” and “evening” periods, whereas the “afternoon” period was characterized by drowsiness with much sitting and occasional feeding. These patterns resembled those described by Beer (1961) for free-living winter flocks of House Sparrows. The last half-hour of light was one of great vocal and aggressive activity resembling natural pre-roosting behavior. Although these be-

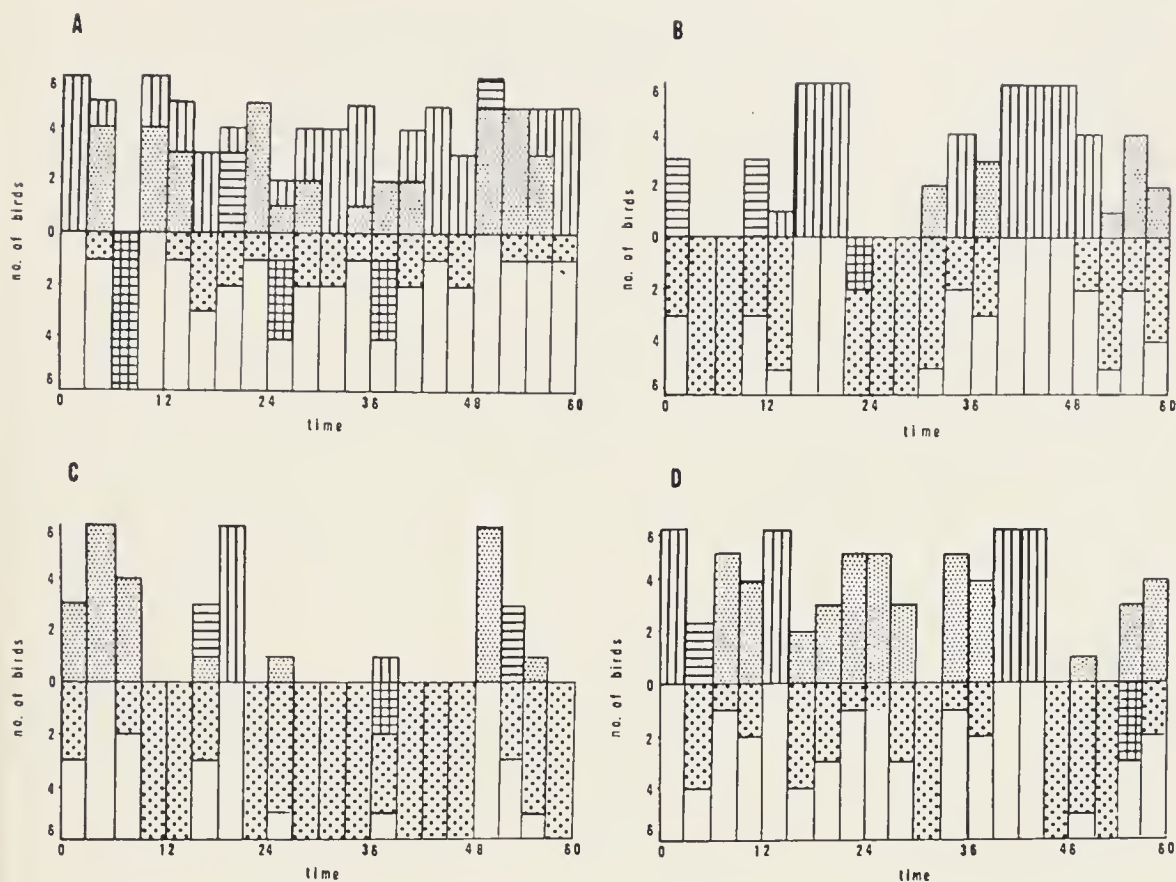


FIG. 2. Recording of group activity cycle of House Sparrows from the June-July flock (Table 2, group 5). Six birds observed for 60 minutes from 07:00-08:00. (A), 10:30-11:30. (B), 13:30-14:30. (C), 17:00-18:00. (D). Observations were made at the beginning of each three minute period. Key: Feeding—Small dots; Hopping—Horizontal bars; Flying—Vertical bars; Sitting—Large dots; Feather care—Cross bars.

havioral adjustments were made under artificial conditions, they served to establish a cyclic context from which observations could be interpreted. As stated by Moynihan and Hall (1953), the motivation of a specific behavior pattern was considered to be the same, whether performed in a cage or in the wild.

In these experiments, the alpha male showed a marked tendency to divorce himself from flock activities. This bird showed little tendency to follow others and no marked potential for initiating new flock activities. When not fighting, the alpha male could be identified by his behavior of sitting lethargically in one place and not participating in flock activities.

Data from the April group (Table 2, 8a) showed A dominant over B. Out of 226 flights by A, individual B followed 158 times. Conversely, out of 606 flights by B, male A followed only 32 times. The greater number of flights by B was attributed to the great nervousness of the bird. In this case, the sub-

ordinate did follow the alpha male a significant number of times. However, this was probably the result of a small opportunity for alternate action coupled with the nervousness of B. Also, the passive behavior of the alpha male was a factor. In larger groups ($N = 6$ to 8), all birds showed an equal potential for elicitation of new activities (based on qualitative notes).

DISCUSSION

The dominance-subordination relationships of highly gregarious species of birds have been subject to much speculation. Schjelderup-Ebbe (1933) stated that beyond 10 individuals, straight-line hierarchies rarely exist. Conversely, Guhl (1953) gave evidence for a hierarchy in a flock of 96 pullets. Sabine (1959) described a scale of dominance for a flock (that resulted from the amalgamation of two flocks) of 42 Oregon Juncos (*Junco oreganus*). However, it would seem that these flock sizes represent the extreme upper limits for individual meeting and acquaintance to occur.

Whether the results of investigations using small numbers apply equally well to larger flocks was questioned by Banks and Allee (1957). It seems reasonable, however, that if a hierarchy is nonexistent in small flocks one would not exist in larger flocks of the same species.

No obvious linear hierarchy existed with the captive sparrows. For example, Table 3 (April group) indicates a peck rank for three adult males (A 66/72, B 6/72, C 0/268). The disproportionate defeats assumed by C were due to his lack of a defended site. However, B, who did maintain a specific site at which he remained, was largely free from attacks and managed to defeat A 6 times at this location. Therefore, the situation revealed reversible site-related dominance among the males. Since the black bill color was lost by the captive males indicating gonadal regression (Keck, 1932) and no sexual displays were seen, reproductive complications were minimized.

Instances of caged birds establishing separate territories have been recorded for a few species (Shoemaker, 1939; Ritchey, 1951). In caged groups of House Finches, the alpha pair defended the entire aviary with the beta pair defending the same area but with less aggressiveness (Thompson, 1960). However, Ellis (1966) showed a hierarchy independent of site relationships in captive groups of Starlings. In my experiments, the alpha male exerted his influence over the largest area somewhat resembling the behavior of the caged House Finch but the sparrow aggression was not related to pair nest defense, and the other male sparrows did not defend the same area. The situation seemed to agree with the findings of Ritchey (1951) who stated that in caged groups of domestic pigeons, a linear hierarchy was blocked by site-related dominance.

The results of this captive study may relate to certain events occurring under natural conditions. As stated by Dixon (1965), reversible, site-related responses between individuals have little value in promoting group unity. Free-living adult male sparrows maintain one specific site for both the breeding and non-breeding season (Summers-Smith, 1963). However, the intensity of intolerance exerted in defense of these sites during the non-breeding season is unclear. In any event, this type of site-related aggression would have questionable significance in large flocks of foraging sparrows. When on neutral ground, an attacking sparrow seems to have the advantage over the recipient (notwithstanding "stay threat" behavior). This situation was apparent in the large floor feeder where aggression was rare. Reduced aggression at the feeder has also been reported for caged groups of Goldfinches (*Spinus tristis*) by Coutlee (1967).

SUMMARY

Dominance-subordination relationships were studied in 8 groups (2-8 individuals per group) of captive House Sparrows between January and September, 1965. In each group a highly combative male won the majority of contests, but a linear hierarchy was blocked by reversible site-related dominance. The significance of site-related aggression in large flocks of foraging House Sparrows is questioned. The adult females rarely fought among themselves and were largely free from adult male aggression. First-year birds were treated as adult females by adults of both sexes. However, when attacked they demonstrated "stay threat" behavior. "Stay threat" was characterized by the first-year birds actively defending their positions when attacked without pressing the encounter beyond the immediate site.

Activity patterns were greatest during "morning" and "evening" periods with a characteristic "mid-day lull." The birds tended to engage in the same activities at the same time. The top-ranking adult male showed a tendency to divorce himself from the flock and demonstrated no marked potential for initiating new flock activities.

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